Patterns and processes in freshwater systems: the social dimension

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Abstract

Social interactions within species present an under-appreciated complicating factor in freshwater ecology. Such processes can markedly alter distribution patterns. Odonata are an important group of animals in freshwater systems and have the capacity, under some circumstances, to exclude other organisms (invertebrate and vertebrate) from otherwise suitable habitats. Within the Odonata stylised agonistic behaviours are widespread in larvae of Zygoptera and have important consequences for both the ecology of the species concerned and for the impact of zygopteran larvae within ecosystems. In this paper the diversity of agonistic displays within the Zygoptera is reviewed. On phylogenetic grounds, supported by fossil dates, zygopteran display systems are very ancient (~ 150-200 My). Given the obvious costs in energy, increased exposure to predators, and the real risk of damage during interactions, agonistic behaviours must have considerable adaptive significance. Investigations of the processes involved in social interactions, and how they generate the patterns that are more generally recorded, will probably require a return to large aquarium studies, or to in situ examination of microhabitats using underwater observatories.

Keywords: freshwater ecology - Zygoptera larvae - interactions - agonistic behaviour.

Introduction

Ecology is a difficult and complex science. In its current guise it evolved after Relativity (both the special and the general theories), after Quantum Mechanics, and after the development of modern Statistics. As a science, ecology needs to handle the particular (for every system is in some way unique) and also to allow for stochastic variability about some notional resting or equilibrium value... all under conditions where the system is dynamically shifting even as it is measured. No two tides are ever the same. As Heraclitus (*c.*535-475 BCE) tartly observed 'you can't enter the same river twice'. Yet there are patterns in the natural world, and it is important, and even useful, to find them.

Ecologists have attempted to discern patterns in the swirl of space and time using three complementary techniques: correlative studies, manipulations

('experiments') and knowledge of fundamental underlying biological processes. The first of these is exemplified in freshwater studies by widescale 'sampling' exercises, where fauna and flora are collected and their numbers (biomass or life-history stage) correlated with both physical and biogeographic data, and 'internally' with biological data concerning other members of the community. Broad scale patterns are sought by sampling, the data then being integrated to 'average-out' irrelevant fluctuations, and thus to improve the signal to noise ratio. Experimental manipulation follows to 'test' the patterns found. Common manipulations include habitat modification (physical and / or chemical), enclosure and exclosure cages, controlled 'artificial streams' (or ponds) and in situ nutrient level modification.

The third leg of the analytical tripod is currently less well-followed. Fifty years ago theses, papers, and even monographs on 'The Life of X' were not uncommon. Such science has fallen desperately out of fashion. Yet, the data from such studies are fundamental to building up, from first principles, as it were, a model of the system. Modelling itself is currently very fashionable, but collection of the sorts of data required to build a solid foundation for the extrapolations and speculations of modelling is not.

In essence, the first two methods combine in an attempt to distill information on process from pattern using correlative measures and inductive reasoning. The third method attempts to extrapolate from basic processes to wide-scale pattern using modelling methods. In a perfect world the results of the different methodologies would mesh together seemlessly. To progress efficiently scientists need to move between these three viewpoints.

A further, fundamental, problem on how to seek, and interpret, pattern and process in ecological data can be traced back to seminal papers by Hutchinson (1959) and Lewin (1983). Hutchinson (1959) argued for the importance of biological interactions in determining ecosystem structures; Lewin scathingly demolished Hutchinson's arguments. The follow-up arguments in this debate generated a lot of heat, and in retrospect, not that much light, possibly because the questions were really at different levels and as such incommensurable. The arguments are irresolvable…but as an animal behaviourist I am fascinated by the diversity and complexity of predator-thwarting behaviours. To me the evolution and maintenance of such specialised, and often costly, behaviours point to the importance of biotic interactions.

Because of the diversity of biological systems being investigated, and the frequently shifting sands of the underlying notional objective(s) of the research programes, it is important for scientists to tie ecological studies to some concrete exemplar or exemplars, and thereby to provide a link to a reality. Theoretical ecology on imaginary animals can sometimes be useful (Sheldon & Kerr 1972), but often theoretical ecology on imaginary animals living in virtual universes is carried out in good faith by scientists unaware of how far they have drifted from empirical support.

Odonata larvae as a paradigm

Larval Odonata provide a well defined and well researched exemplar from which to extrapolate research programmes. The literature is synthesised in three

complementary reviews by Corbet (Corbet 1962; 1980; 1999). In essence, Odonata larvae are medium to large-sized, almost invariably freshwater insects that are obligate predators, able to attack and consume a wide range of invertebrate prey, and with the larger species also consuming smaller vertebrates. Predatory competence is dependent on the detailed organisation of the predatory structures (which varies among lineages) and on behavioural aspects. Prey is acquired by the rapid extension of the highly modified labium, which acts as a strike and capture device. Larvae occur in almost all shallow, freshwater habitats. Members of the suborder Zygoptera are especially prevalent in vegetated lentic habitats, whereas in running waters a range of different zygopteran species occupy both vegetated areas and bare stone surfaces. Microhabitat specialisation occurs at family, generic and species levels.

Odonata larvae can have a marked effect on other organisms within their habitats. Frequently, they have a high standing biomass, which when coupled with both a low basal metabolic rate and the ability to handle very large quantities of food rapidly, should it become available, makes them potentially important components of the biotic system. Most species normally handle food items up to about one third their own mass, but some species regularly attack and overpower prey with a body mass roughly equivalent to their own (unpubl. obs.). At the other end of the scale, many species capture and feed on prey about one thousandth their own body mass and effectively act as vacuum cleaners removing the smaller life-history stages of organisms.

Under normal conditions, too few scientists ask about what is not in a habitat, despite the capacity for odonate larvae to entirely remove faunal components being documented. In tropical Australia, dragonfly larvae (*Pantala flavescens*) have a considerable impact on the barramundi (*Lates calcarifer*) aquaculture industry. Thus, attempts to raise this large gamefish in extensive, hectare-sized, semi-natural freshwater ponds were completely unsuccessful as dragonfly larvae exterminated the small, but quick-growing fry. Fry needed to be grown in protected conditions to a length of 17 mm before they could survive in the freshwater ponds (Mackinnon 1989). (Barramundi normally lay eggs in brackish estuarine waters that are too saline for most predatory dragonflies). Other examples of the elimination of vulnerable prey species are known. Looking for what is not there is not necessarily a pointless exercise.

The predatory capabilities of odonate larvae make details of their general ecology, microhabitat selection, and behaviour important for understanding the dynamics of the freshwater ecosystems of which they are a part. Based on observations of community structure Macan (1977) proposed that zygopteran larvae may be spread out and uniformly distributed within habitats, and in the same year Machado (1977) observed that larvae of a damselfly *Roppaneura beckeri* were expelled, presumably by other larvae, from the limited habitats provided by phytotelmata, with 'losers' emigrating to other water-filled leaf axils. Subsequently, Rowe (1978; 1980; 1985a; 1992a) identified a rich display repertoire and complex interactions associated with intraspecific agonistic behaviour in *Xanthocnemis zealandica*, processes which could have generated the patterns inferred and observed in other species by Macan

(1977) and Machado (1977).

Since then, complex agonistic behaviour, involving specialised postures and actions ritualised and modified for communication, have been observed in many zygopteran lineages (e.g., Rowe 1980; 1985a; 1987; 1992a; 1992b; 1993; 1994; 2004; Baker 1981; Finke 1996; Harvey and Corbet 1986; Richardson and Anholt 1995; Ryazanova and Mazokhin-Porshnyakov 1992; Sant and New 1989). Even taxa that appeared to have few displays (e.g., *Austrolestes colensonis* – Rowe 1985a) have on re-examination proved to have diverse repertoires (Rowe 1992b), and species reputed to 'fight to the death' (Finke 1984) have later been filmed displaying in a ritualised fashion (Attenborough 1990) and their display repertoires documented (Finke 1996).

Agonistic behaviour

Agonistic behaviour runs deep. On biogeographical grounds (opening of the Atlantic, breakup of Gondwana) some odonate lineages, such as the 'superfamily' Lestoidea, retain common displays from at least 120-150 Mya. A trace fossil from the late Triassic (Rozefelds 1985) strongly resembles a synlestid, so this lineage may have an independent history (and probably retained agonistic behaviours) dating to over 200 My. Other groups present interpretational problems because of the state of flux of conventional taxonomies (e.g., Bechly 1995; Trueman 1996; Rehn 2003). In well defined groups there is certainly a high level of phylogenetic inertia in display repertoires, which opens the prospect of using agonistic behaviours in phylogenetic reconstruction (e.g., Rowe 1993; 1994; 2003; 2004). Two enigmatic taxa – the Pseudostigmatidae (giant helicopter damselflies of the tropical Americas) and *Hemiphlebia mirabilis* (an Australian relict, once viewed as an isolate and sister group to the remaining Odonata) – have been linked to the Coenagrionidae and to the superfamily Lestoidea, respectively on the basis of larval agonistic behaviour (viewing of Attenborough 1990; Sant and New 1988). Furthermore, these agonistic behaviour-based assignments are consistent with the most recent morphological and molecular sequence analyses (Bechly 1995; Rehn 2003; Trueman pers. comm.).

The complexity of agonistic behaviour repertoires varies somewhat. Some postures and actions are highly modified from their proposed 'ancestral state', whereas others vary little from functional actions. For example, almost all species examined have some modification of the labial predatory strike in their display repertoire: whereas the functional action is invariably well-ranged and targeted, and prey is impaled or grasped, when used as a display this action is variously triggered out of range, directed to miss the opponent, aimed at a conventional target (caudal lamellae, especially badges on same) or has no, or only a limited, grasping component (Figure 1). However, in some species, opponents are occasionally attacked using the labial strike and may be injured or killed (Baker & Dixon 1986; Fincke 1984). Ritualisation may only go so far.

In species examined in detail the repertoire of major displays (*sensu* Moynihan 1970) typically has around 20 - 25 elements. However, there are also ontogenetic shifts in repertoire to be considered (Rowe 1992a, Richardson & Anholt 1995), which increase total repertoire size. Calopterygids and lestids appear to have smaller repertoires than

coenagrionids. Some elements in families best regarded for the moment as insertae sedis (e.g., Amphipterygidae, perhaps 'Diphlebiidae'?) have large, well-developed, and seemingly distinct display repertoires.

Display repertoires are rich. At any one time a typical coenagrionid larva seems to have around 20 displays 'operational' (Rowe 1992a; 2002; 2003; Richardson & Anholt 1995). Because of the prevalence of 'asymmetric encounters' between animals of different size we must presume an animal 'recognises' at least some displays of both smaller and larger larvae (e.g., Rowe 1992a; Richardson & Anholt 1995) that are not in its own current repertoire. The size of the individual agonistic display repertoire of a typical coenagrionid damselfly larva is about the same as the known communication repertoires of small mammals and other small and medium-sized vertebrates (reviews in Wilson 1975; Bradbury & Vehrencamp 1998). These displays and actions are recognised and rapidly processed (with signal / response latencies in some cases below 0.04 s), by a brain the size of a pinhead.

To the 40-odd total displays and actions documented for members of the Coenagrionidae can be added another three novel displays in the Isostictidae (Rowe 1994), about 12 in the superfamily Lestoidea, three in the Amphipterygidae (*Diphlebia*, Rowe 1993) and three in the Calopterygidae. Thus, some 60-odd displays, actions, or novel combinations of displays and actions are currently recognised in larval Zygoptera. It is to be anticipated that further displays will be recognised as coverage of these communication systems expands across the available taxa, and deepens with more detailed studies within taxa, especially in the thorough coverage of ontogenetic shifts. Total repertoire size within the suborder Zygoptera is truly prodigious when the limited common pool of precursor behaviours, and the actually realisable stances available to a rigid-exoskeletoned arthropod, are considered. Displays are evolutionarily important to this group.

Time spent displaying also varies. In all species examined most contests last only a few seconds, if that. However, under some conditions (e.g., in *Xanthocnemis zealandica*: Figure 2) contests may involve

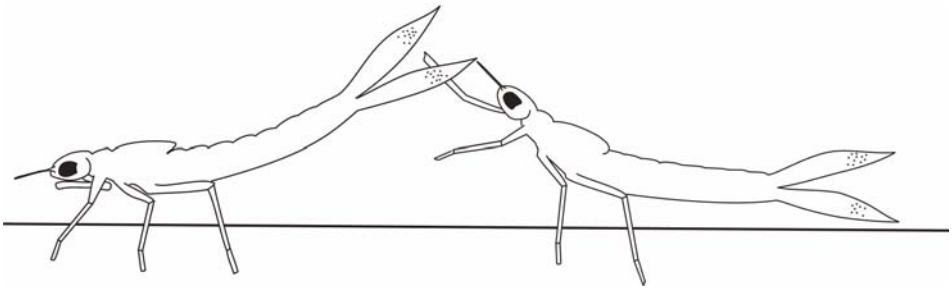

Figure 1. Ritualised use of the labial strike in *Xanthocnemis zealandica* intraspecific contests. The target animal is far too large to be prey, the strike is aimed (with some contortion) at the badge on the caudal lamellae, the target is barely within range and is struck and not grasped. In this species predatory attacks are on animals significantly smaller than the predator, the strike is aimed at the body (or the head) of the prey, and the labial palps and hooks grasp the target. (F-3 instar larvae, drawn from a video frame; see Rowe 1992a).

a succession of bouts, each taking upwards of an hour, and extend over several days (Rowe 1985b). These patterns are characteristic of agonistic interactions in general, with most 'contests' being settled quickly, and with long-lasting 'wars-of-attrition' occurring only in exceptional circumstances.

Consequences of agonistic displays for Zygoptera

The costs of displays, and especially of agonistic display systems, are widely documented (e.g., Bradbury & Vehrencamp 1998). They can be condensed into four main components: (a) opportunity costs associated with loss of time when the animal could be doing something else together with associated costs of the forgone benefits that could accrue during these alternative activities, (b) energy costs of displaying, (c) mortality risks associated with displays attracting predators, and (d) injury and mortality risks arising from displays converting into escalated contests. In zygopteran larvae the 'alternative activity' in (a) is hunting for prey. For a sit-and-wait, ambush predator like *X. zealandica* this is a leisurely process over which the larva has little control, but for active foragers, as at least some other species seemingly are, there may be a real cost in time lost to displaying. Activity during displays (b) is some of the most energetic activity found in zygopteran larvae, but for most species the time spent displaying and the energy requirements above the basal metabolic rate are unlikely to be a major burden.

In contrast to the first two 'costs', the risks associated with displays are significant. Displaying larvae are generally fairly obvious (c), and in aquaria, predators such as aeshnid larvae, have been seen to 'spot' displaying zygopteran larvae and then to stalk them. It is easy to extrapolate such observations into potential field contexts. There are many

Figure 2. *Xanthocnemis zealandica* larva on perch. Photo: Michelle Greenwood.

predators. To reduce the risk of being eaten zygopteran larvae may suppress agonistic displays in the presence of predators. This has been observed in *X. zealandica* larvae in the presence of dytiscid larvae (*Rhantus suturalis*) (Rowe 1985b) and casually when larvae were in aquaria in the presence of fish. McPeek (1990) tested larvae of four closely related *Enallagma* species, two species each from lakes with fish or with aeshnid larvae as 'top predators'. His results showed the species from 'fish' lakes did not use abdomen waving displays, and that one of the species from 'aeshnid' lakes strongly suppressed the use of the display in the presence of aeshnid larvae. This is consistent with predators attracted to displays being a significant selection pressure on the larvae.

In most species investigated, escalated contests and damage (d) are very rare occurrences, but at least in some species this does happen. Baker & Dixon (1986) provided a measure of intraspecific damage done in the field, demonstrating that the processes involved were not an artifact of the limited areas or reduced escape opportunities available in aquaria. The Baker and Dixon (1986) work showed that levels of wounding correlated positively with population densities and that the wounds observed (mainly loss of caudal lamellae) were consistent with those that animals suffered in escalated aquarium contests. Ritualisation of agonistic interactions, with consequent reduction in the risk of sustaining injury in combat, is a strong prediction of various hawk-dove models for selection in agonistic situations (Maynard Smith & Price 1973). 'Posture' or 'retaliate' are predicted to be evolutionarily stable strategies, and this seems borne out for the most part in observations of zygopteran larval contests ... with the caution that in rare, longer-duration, obviously escalated contests potentially damaging attacks can, and do, occur.

The benefits of agonistic behaviour must be considerable given it is maintained in the face of actual and potentially considerable costs. However, searches for 'the benefit' are not necessarily easy. The benefit(s) for animals that sit on stems for long periods (such as *Xanthocnemis zealandica* in natural and artificial reed beds [Rowe 1985b]) are hardly likely to be the same as those for animals that spend the day in refuges and emerge at night to hunt on stone surfaces (e.g., *Neosticta fraseri* (Rowe 1994), *Diphlebia euphoeoides* (Rowe 1993), synlestids (Rowe 2004), and probably calopterygids. Animals that move around within a habitat, without evidence of localising (e.g., *Megaloprepus* [Finke 1996], *Austrolestes colensonis* [Rowe 1992b], *Ischnura* species [Rowe 1985a; Crowley 1979] and perhaps *Xanthocnemis zealandica* in weed beds), are unlikely to be receiving the same benefits as those that defend long-term perches.

Furthermore, the benefits of agonistic behaviour may vary with development as the larvae change both microhabitat and ecology (Corbet 1999). That small larvae of many species have well developed agonistic repertoires, which develop ontogenetically (Rowe 1992a; Richardson & Anholt 1995) in a manner I interpret as being consistent with the development of their sensory capabilities, is evidence for a benefit or benefits during these earliest free-living life history stages. Such benefits may differ markedly from those received in later instars. Small larvae of many coenagrionid species have very similar behavioural repertoires (unpubl. obs.). Whether this is associated with

occupation of similar microhabitats, the common constraints of their sensory systems, or perhaps because of a tendency for specialisation and 'novelty' to be added at the end of developmental chains (Gould 1977) is probably unresolvable unless serendipidy presents us with some phylogenetically well-separated peculiarities that could serve to break the impass.

The first damselfly in which patterns of agonistic behaviour were investigated was *Xanthocnemis zealandica* (Rowe 1978; 1980). In this species larvae localise on perches for long periods of time. Durations of undisturbed second-instar larval site occupation followed an exponential decay pattern with a half-life of 30-35 h, and with some animals sitting on the same site for over 150 h of the approximately 250 h duration of the stadium (Rowe 1985b). A similar tendency to 'stay put' was observed throughout the larval life history, with some diapausing animals remaining on a single site for upwards of 80 days, and other individuals remaining on a site across two moults (Rowe 1985b). When the larvae are on stems they spend almost all their time within a few centimetres of the bottom, facing down. Very occasionally, they may 'patrol' their stem, climbing perhaps to the water surface, before returning and resettling near the base. Patrols rarely last more than an hour.

Animals on stems may leave their perches to retrieve nearby carrion, walking past other stems to reach their target. After acquiring the carcase they drag or carry it back to their original stem where they consume it, sometimes over a period of days. The unconsumed food is dropped to lie at the base of the stem at the end of each feeding bout and retrieved to begin a new meal. There is a high level of stem fidelity in these animals.

On their stems, small resident animals may attack larger intruders vigorously, and with alacrity, quickly driving the invader from the perch. On a few occasions in the laboratory a resident animal was seen to be driven from its perch by a similar-sized intruder, only to move a short distance (5-10 cm) before turning about, returning to its original perch and evicting the invader, thereafter retaining occupancy.

In *X. zealandica* in reedbeds the observed behaviour clearly meets all reasonable definitions of there being territorial behaviour. In contrast, in other species with different ecologies, equally clearly the behaviour represents a size-mediated dominance relationship (Finke 1996). No work has yet been done to establish whether in the later case there is any longer term memory of outcomes of previous contests, or whether a stable social hierarchy develops, as in many other animals.

Alternative signal channels

When discussing displays we tend to describe the motor patterns casually as if they were visual displays. But night being half the day (and often the more important part) this should be interpreted with caution: communication via the display motor patterns observed and described may be by vibrational sensory channels (either sound or water movement in displacement waves). In small larvae, vibration (and probably the displacement wave sense), is the most likely sensory channel because of their limited visual capacity; but for larger larvae the explanation is less obvious. The

anisozygopteran / basal anisopteran *Epiophlebia superstes* has, and uses, a complex stridulatory organ (Asahina 1938; 1939), and during exploratory studies in my laboratory hydrophones have picked up snapping and grating 'noises' occurring concurrent with displays in zygopterans. Particle movement, obvious in videotapes of displays, provides evidence of broadscale displacement waves associated with interactions. Nevertheless, the possibility that there are visual components to these displays should not be completely rejected. The visual capabilities of insect apposition compound eyes under low light conditions can be remarkably effective, in some cases operating at levels as low as 10^{-4} cd m^{-2} (i.e., approximating starlight) and have been reviewed by Warrant (2004). A good low light visual competence is consistent with the activities of tropical dragonfly larvae, which emerge from rainforest streams at night to hunt on the banks and over leaf litter, in an environment, and under conditions, where vision seems the only sense available to them. The possibilities of synergistic multi-channel communication require investigation.

Potential community level consequences

Lastly, is all this displaying, the aggression, the submission, the placatory displaying, of any interest other than to the parties involved? Yes. The consequences within the community of uniformly distributed predators, rather than those following an ideal free distribution (Fretwell & Lucas 1970), are different. Predators following something approaching an ideal free distribution will aggregate in areas where common prey abound (i.e., moving such that the expected rate of return to each individual predator is the same); in contrast, predators distributed uniformly throughout the habitat will have a much higher relative impact on rarer prey species (either because they themselves are dispersed or because there are predators in their refuge areas). This whole field of study began with Macan's (1977) inferences based on an analysis of the impact of predators in shaping freshwater communities. Initially, he observed that in years of high abundance, but not in other years, the larval cohort of the damselfly *Pyrrhosoma nymphula* comprised two size-classes – uniformly large individuals and a group of smaller animals. He interpreted this division as evidence of social monopolisation of feeding areas, with excluded animals becoming 'runts'. He then looked for correlations that would be consistent with such a pattern and noticed that predatory flatworms were absent from ponds with *Pyrrhosoma*. Antisera tests had shown that *Pyrrhosoma* often fed on flatworms, and enclosure / exclosure experiments confirmed that *Pyrrhosoma* larvae could exclude planarians from habitats. The social system Macan (1997) inferred from the split in the cohort in "high-density years" is likely to have been sufficient to enable distribution of *Pyrrhosoma* larvae throughout the habitat, leaving no refuges for flatworms. In developing his argument and reaching his conclusions Macan had both wide experience in the field and crucially, extensive data extending over a period of more than 20 years (e.g., Macan 1974; 1976). When looking at patterns and attempting to infer process, long term studies are invaluable, and there is no substitute for them.

The hard question that should concern

us is: are Zygoptera in any way unusual other than that they have been looked at? At night take a good torch to any clear stream or pond and peer into the water... you will see a rich and diverse insect fauna, doggedly going about its business, seemingly oblivious to the intrusion. The fundamental problem is we do not know enough about what animals do. We know gross things: this animal occurs in lakes, ponds, rivers or perhaps streams. We may even 'know' that an animal 'occurs' in weedbeds, or in sand, or among cobbles. But very rarely do we know the spatial and temporal microhabitat occupied, or the way the animal uses its habitat. The rare exceptions to this lack of knowledge are generally associated with sedentary animals (e.g., simuliid larvae [Chance & Craig 1986] and hydropsychid larvae [Harding 1997]), and indicate a very high level of microhabitat specificity. Furthermore, in both these groups of insects, social interations (e.g., Jansson & Vuoristo 1979) are known to be important determinants of distribution patterns within larval microhabitats.

Investigations into the processes involved in social interactions, and how they generate the patterns that are more generally recorded with 'standard' methods like daytime dip-netting or Surber sampling, will probably require a return to large aquarium studies, or to in situ examination of microhabitats using underwater observatories (Bay 1974; construction design in Strong 1972). To find what animals are doing we will have to enter their world.

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